

# Punishment can promote defection in group-structured populations

Simon T. Powers<sup>a,1,\*</sup>, Daniel J. Taylor<sup>a</sup>, Joanna J. Bryson<sup>a</sup>

<sup>a</sup>*Department of Computer Science, University of Bath, Bath BA2 7AY, UK*

---

## Abstract

Pro-social punishment, whereby cooperators punish defectors, is often suggested as a mechanism that maintains cooperation in large human groups. Importantly, models that support this idea have to date only allowed defectors to be the target of punishment. However, recent empirical work has demonstrated the existence of anti-social punishment in public goods games. That is, individuals that defect have been found to also punish cooperators. Some recent theoretical studies have found that such anti-social punishment can prevent the evolution of pro-social punishment and cooperation. However, the evolution of anti-social punishment in group-structured populations has not been formally addressed. Previous work has informally argued that group-structure must favour pro-social punishment. Here we formally investigate how two demographic factors, group size and dispersal frequency, affect selection pressures on pro- and anti-social punishment. Contrary to the suggestions of previous work, we find that anti-social punishment can prevent the evolution of pro-social punishment and cooperation under a range of group structures. Given that anti-social punishment has now been found in all studied extant human cultures, the claims of previous models showing the co-evolution of pro-social punishment and cooperation in group-structured populations should be re-evaluated. [This is a post-print of an accepted manuscript published in *Journal of Theoretical Biology* 311 (2012) 107–116. The publisher's version is available from <http://www.sciencedirect.com/science/article/pii/S002251931200344X>.]

**Keywords:** anti-social punishment, equilibrium selection, public goods, behavioural economics, strong reciprocity

---

## 1. Introduction

Understanding the evolution of individually-costly cooperative behaviours is a major focus of social evolution theory (Hamilton, 1964; Wilson, 1975; Frank, 1998; Lehmann and Keller, 2006; West et al., 2007; Archetti and Scheuring, 2012). It is now

---

\*Corresponding author

*Email addresses:* [Simon.Powers@unil.ch](mailto:Simon.Powers@unil.ch) (Simon T. Powers), [D.J.Taylor@bath.ac.uk](mailto:D.J.Taylor@bath.ac.uk) (Daniel J. Taylor), [J.J.Bryson@bath.ac.uk](mailto:J.J.Bryson@bath.ac.uk) (Joanna J. Bryson)

<sup>1</sup>Present address: Department of Ecology & Evolution, Biophore, University of Lausanne, CH-1015 Lausanne, Switzerland

*Preprint submitted to Journal of Theoretical Biology*

*March 8, 2013*

widely appreciated that cooperative behaviours can evolve if they provide either a direct fitness benefit to the actor during its lifetime, or if they provide an indirect fitness benefit by helping other cooperators (e.g. relatives, Hamilton, 1964; Lehmann and Keller, 2006; West et al., 2007). A great deal of current research is aimed at understanding the biological mechanisms that provide direct or indirect fitness benefits in different scenarios (Hammerstein, 2003; West et al., 2007). In particular, identifying the mechanisms that provide direct or indirect fitness benefits to cooperators in large human groups, where genetic relatedness is typically low, remains an open challenge. This question has received much attention, due to the fact that humans appear to cooperate on a much larger scale than other species, and thus large-scale cooperation seems to be one of the properties that make human sociality unique.

Cooperation in humans is often framed in terms of the production and sharing of various public goods. This may take the form of, for example, sharing food or information with other group members, or contributing time, energy, and resources to a group project. Throughout this paper, we focus on social dilemmas that take the form of *linear public goods games*<sup>2</sup>. In linear public goods games (PGG) there is an apparent individual advantage to defection, that is, to reaping the benefits of the public good without paying the individual costs of contributing to it. We would expect such defectors to be fitter than cooperators within the same group, and hence for natural selection to lead to the breakdown of cooperation in a “Tragedy of the Commons” (Hardin, 1968). However, we see that cooperation is nevertheless maintained in large human groups despite the apparent advantage of defection. Explaining this is problematic because many cases of cooperation in humans occur in large groups of unrelated individuals.

Punishment behaviours have been widely suggested as a solution to this quandary. In particular, cooperative individuals may have the option of punishing defectors. Typically, punishment takes the form of an actor paying a cost by reducing its own fitness in order to reduce the fitness of the punishment target, as in the following fitness functions:

$$w_d = 1 + Bx_p - Px_p \quad (1)$$

$$w_p = 1 + Bx_p - C - Kx_d, \quad (2)$$

where  $w_d$  is the fitness of defectors, and  $w_p$  the fitness of pro-social punishers (individuals who cooperate and then punish any group member that defected). In these functions  $B$  is a constant representing the benefit that a single cooperator provides,  $C$  the cost of cooperation,  $P$  a constant representing the cost of being punished, and  $K$  the cost of punishing an individual. The constant 1 represents a baseline fitness in the absence of social interactions.

The proportions of defectors and pro-social punishers within a group are denoted by  $x_d$  and  $x_p$ , respectively. The relative cost of  $P$  and  $K$  is subject to some debate, however, empirical evidence from PGG experiments show similar effects for a range of relative values (Anderson and Putterman, 2006). In the present paper we assume that the cost of being punished is partially distributed, and depends upon the *proportion* of punishers, not the absolute number, in a group. This is a common assumption in models of the evolution of punishment (Boyd and Richerson, 1992; Boyd et al., 2003; Lehmann et al.,

---

<sup>2</sup>See Archetti and Scheuring (2012) for a discussion of the differences between linear and non-linear public goods games and how these affect the selective dynamics of cooperation.

2007). We assume that an individual has a fixed amount of time and energy that can be spent on acts of punishment, and also (as in prior work, Boyd and Richerson, 1992; Boyd et al., 2003) that each punisher punishes every available target in its group, or at least that their cost of punishment is proportional to their probability of encountering punishment targets. The more individuals there are for an actor to punish, the less effort the actor can exert on punishing any one individual, and hence the less absolute damage is inflicted per punisher per target. Note that in most literature, punishment targets are taken to be defectors, but in the case of anti-social punishment targets may be cooperators.

In the above typical model, when pro-social punishers are sufficiently common within a group, it is individually advantageous for potential defectors to switch behaviour to cooperating. The condition for this is  $Px_p > Kx_d + C$ , that is, when punishers are in sufficient frequency that the cost of punishing and cooperating (i.e. being a pro-social punisher) is less than the cost of being punished (Lehmann et al., 2007). Thus, in this simple model the evolutionarily stable states are either pro-social punishment at fixation, or defection at fixation. Note that this result holds even in a well-mixed population, and so would be applicable to large groups of unrelated individuals (Boyd and Richerson, 1992).

There are, however, at least three problems with this as a mechanism for the maintenance of cooperation in human groups. The first is that because both pro-social punishment and defection are equilibria, why would we expect natural selection to lead to one rather than the other (Boyd et al., 2003)? It has been argued that group selection (in the broad sense, Okasha, 2006) should promote the pro-social punishment equilibrium (Boyd et al., 2003; Bowles and Gintis, 2004), because this increases the mean fitness of group members. The second problem is that pro-social punishment may not actually be stable under mutation if cooperation and punishment are not perfectly linked traits (Lehmann et al., 2007). This is because pro-social punishers may be slowly replaced by non-punishing cooperators that do not pay the cost of punishing, and who are not themselves punished (the second-order free-riding problem, Colman, 2006). As pro-social punishers decline in frequency due to the accumulation of non-punish mutations, defection may again become advantageous. The third problem is that there is no reason to suppose that only defectors can be targets of punishment: defectors may have the option of punishing cooperators, as evidenced by recent empirical work (Herrmann et al., 2008). Exploring the consequences of this third problem, termed *anti-social punishment* (ASP) motivates the present investigation.

Recent theoretical work (Rand et al., 2010; Rand and Nowak, 2011) has suggested that anti-social punishment can thwart the evolution of pro-social punishment and cooperation. However, no study has formally addressed anti-social punishment in group-structured populations, even though such population structures are frequently modelled when considering the evolution of pro-social punishment (Boyd et al., 2003, 2010; Bowles and Gintis, 2004; Lehmann et al., 2007). Group-structured populations are an essential component of cultural group selection, and of recent arguments about punishment promoting group-beneficial cultural norms in humans (Boyd et al., 2003; Gintis et al., 2003; Mathew and Boyd, 2011; Sober and Wilson, 1998). Thus such populations warrant an explicit model in order to determine whether the inclusion of anti-social punishment affects the claims of these works. For example, some previous work has verbally argued that the presence of group-structure should be expected to favour pro-social punishment

even when anti-social punishment is present (Rand et al., 2010; Rand and Nowak, 2011). According to this view, we might not expect anti-social punishment to have any effect in group-structured populations. Clearly, the implications for the understanding of the proximate mechanisms promoting cooperation in humans motivate a formal examination of this case.

In this paper, we formally address the evolution of anti-social punishment in group-structured populations, focusing on the conditions under which it prevents the evolution of pro-social punishment. We also consider the effects of non-punishing cooperator and defector mutations.

## 2. A model of the evolution of pro- and anti-social punishment in group-structured populations

We consider here a population of individuals that live and reproduce in social groups for a number of generations. In each generation, the following two-phase social interaction occurs and determines fitness within the group. Firstly, each individual either cooperates by paying an individual cost to contribute to a public good, or defects by not contributing. All group members then receive an equal share of the benefit of this good, regardless of whether they cooperated in its production or not. Then, in the second stage individuals have the option of punishing other group members, based on how they behaved in the first stage. We model here the evolution of four behavioural strategies: cooperate but do not punish (non-punishing cooperator); defect but do not punish (non-punishing defector); cooperate and punish all individuals that defected (pro-social punisher); defect and punish all individuals that cooperated (anti-social punisher). The fitness of these four types within a single group is given, respectively, by the following fitness functions:

$$w_c = 1 + B(x_c + x_p) - C - Px_a \quad (3)$$

$$w_d = 1 + B(x_c + x_p) - Px_p \quad (4)$$

$$w_p = 1 + B(x_c + x_p) - C - K(x_d + x_a) - Px_a \quad (5)$$

$$w_a = 1 + B(x_c + x_p) - K(x_c + x_p) - Px_p. \quad (6)$$

Here,  $x_c$ ,  $x_d$ ,  $x_p$  and  $x_a$  are the proportions of non-punishing cooperators, non-punishing defectors, pro-social punishers and anti-social punishers, respectively. As in the previous section,  $B$  is a constant representing the benefit that a single cooperator provides, and  $C$  is a constant representing the cost of cooperation.  $K$  and  $P$  are constants representing the cost of punishing and being punished, respectively. The constant 1 represents a baseline fitness in the absence of social interactions. These fitness functions are based on those commonly used to model the evolution of pro-social punishment (e.g. Boyd et al., 2003; Lehmann et al., 2007), with the addition here of anti-social punishment. Note that in this model, pro-social punishers punish both types of defectors, i.e. non-punishing defectors and anti-social punishers. Likewise, anti-social punishers punish both types of cooperators, i.e. non-punishing cooperators and pro-social punishers.

The number of individuals of type  $i$ ,  $n_i$ , within a group changes deterministically each generation according to the following difference equation:

$$n_i(t+1) = n_i(t) + n_i(t)w_i, \quad (7)$$

where  $t$  refers to the current generation, and  $w_i$  is the fitness of type  $i$  within the group at the current generation, as given by Equations 3–6. Fractional parts are maintained throughout. We assume that reproduction is asexual, and that genotypes are haploid with a single locus determining behaviour. Note that in Equation 7 all individuals of the same type (strategy) within any one group have the same fitness, and reproduce by the same amount. Thus, within groups we do not need to explicitly track each individual, but can simply track type densities.

The above fitness functions describe social interactions within single groups. At the metapopulation level, we model groups formed by random sampling of  $n$  individuals from a global migrant pool of size  $N$ . This sampling is done without replacement, according to a multivariate hypergeometric distribution. Reproduction and selection then occurs deterministically within these groups for  $T$  generations, according to Equation 7. Note that there is no local density regulation in Equation 7, thus, different groups may grow to different sizes over the course of the  $T$  generations. After  $T$  generations dispersal occurs (ecologically, dispersal could be triggered by depletion of a resource patch, for example). During the dispersal stage, a new migrant pool is formed by summing the absolute type densities across all groups. Groups that have grown to a larger size will make up a larger fraction of the new pool, representing a form of global competition between groups. Global population regulation then occurs by proportionality rescaling the migrant pool back to size  $N$ . The number of individuals of a type after population regulation is computed by calculating the proportion of that type in the migrant pool and multiplying by  $N$ , rounding the result to remove fractional parts and produce an integer number of individuals.

Each individual in the migrant pool undergoes mutation with probability  $\mu$ . If chosen for mutation, an individual's genotype is changed randomly to one of the other three types with equal probability. The individuals in the migrant pool then form the next generation of groups (i.e. colonise a new set of resource patches), as previously described. This process of group formation and dispersal then continues for a number of cycles,  $G$ . We simulate the model by the following procedure:

1. **Initialisation:** form a migrant pool of  $N$  individuals with  $N_c$  non-punishing co-operators,  $N_d$  non-punishing defectors,  $N_p$  pro-social punishers and  $N_a$  anti-social punishers.
2. **Group formation:** form  $\lfloor N/n \rfloor$  groups of size  $n$  by random sampling from the migrant pool without replacement (where  $\lfloor \cdot \rfloor$  denotes the mathematical floor function).
3. **Reproduction and selection within groups:** iterate equation 7  $T$  times for each group (see text).
4. **Dispersal:** all individuals leave their groups to form a new migrant pool. The migrant pool is then rescaled back to size  $N$ , keeping the proportion of types the same. Fractional parts are rounded.
5. **Mutation:** each individual in the migrant pool undergoes mutation with probability  $\mu$  (see text).
6. **Iteration:** repeat from step 2 for  $G$  cycles.

The population structure described above is based on the Haystack model (Maynard Smith, 1964; Cohen et al., 1976; Wilson, 1987; Sober and Wilson, 1998; Bergstrom, 2002; Fletcher and Zwick, 2004, 2007; Powers et al., 2011), where we allow

both the size of social groups when they are founded, and the frequency of dispersal, to be parameterised. When  $T = 1$  and dispersal occurs every generation, this corresponds to the well-studied trait-group model of Wilson, (1975; c.f. Hamilton 1975; Michod 1983; Nunney 1985; Maynard Smith and Szathmary 1995; Pepper 2000; Okasha 2006; Santos and Szathmary 2008). This provides us with a simple model that allows the ecological and demographic factors affecting between-group variance, and hence the strength of group selection, to be varied (Sober and Wilson, 1998).

### 3. Results

In this section we show how two demographic factors, group size and dispersal frequency, affect whether selection will favour pro- or anti-social punishment, or no punishment at all. We first present analytical results from a simpler version of the model in which pairs of strategies compete, and dispersal frequency is fixed with groups dispersing after every generation. This population structure corresponds to Wilson’s (1975) trait-group model. It also parallels the anonymous single-shot public goods games used in behavioural economics experiments, particularly those used to study strong reciprocity (Fehr et al., 2002). We then go on to present results from the full simulation model in which all four strategies are present simultaneously, and both dispersal frequency as well as group size is varied. Less frequent dispersal ( $T > 1$ ) corresponds to a Haystack population structure, and is an evolutionary analogue of repeated economic public goods games.

#### 3.1. Analytical results

We explore first the evolutionary dynamics where only two strategies are present in the population at any one time, and where dispersal occurs every generation ( $T = 1$ ). We first note that the fitness of each type is frequency-dependent (Equations 3–6). In particular, the fitness of both pro- and anti-social punishers is positive frequency-dependent. This is because the total cost of punishing decreases as punishers become more common (since less acts of punishment are required), while the total cost of being punished increases (due to more individuals performing punishing acts). Thus, although neither type of punishment may easily be able to invade from rarity (though see Discussion, Section 4), they can be selected for from higher initial frequencies (Lehmann et al., 2007). We therefore focus on how the initial proportion of a strategy required for it to be selectively favoured changes with respect to group size. In addition to the analytical results, we verified each threshold frequency derived below numerically in the simulation model.

##### 3.1.1. Non-punishing cooperators vs. non-punishing defectors

We first consider pairwise competition between non-punishing cooperators and non-punishing defectors. The fitness of each type, given a group containing  $j$  cooperating co-players, is:

$$\begin{aligned}
 w_c(j) &= B \frac{j+1}{n} - C + 1 \\
 &= B \frac{j}{n} + \frac{B}{n} - C + 1 \\
 w_d(j) &= B \frac{j}{n} + 1
 \end{aligned} \tag{8}$$

To calculate whether cooperation increases or decreases in proportion, we need to know the probability distribution  $\mathbb{P}_n(j)$  for an individual to be placed in a group with  $j$  cooperators, given that  $x_c$  is the global frequency of cooperators. In our model, we assume that groups are formed by a random sampling process. In the full model, this sampling occurs without replacement from a finite population according to a hypergeometric distribution. However, for ease of analysis we derive the analytical results in this section by sampling groups from an infinite population with replacement; this does not significantly alter the qualitative behaviour of the results. We thus model group formation in this section by sampling from a binomial distribution.

Let  $g_c$  and  $g_d$  be the fitness of the cooperators and defectors *after* the groups have been formed. We can calculate them by

$$\begin{aligned}
g_c &= \sum_{j=0}^{n-1} \mathbb{P}_n(j) w_c(j) \\
&= \sum_{j=0}^{n-1} \binom{n-1}{j} x_c^j (1-x_c)^{n-1-j} w_c(j) \\
&= x_c B \frac{n-1}{n} + \frac{B}{n} - C + 1 \\
g_d &= \sum_{j=0}^{n-1} \mathbb{P}_n(j) w_d(j) \\
&= \sum_{j=0}^{n-1} \binom{n-1}{j} x_c^j (1-x_c)^{n-1-j} w_d(j) \\
&= x_c B \frac{n-1}{n} + 1,
\end{aligned} \tag{9}$$

where  $x_c$  is the *global* proportion of cooperators. We see that cooperation increases in frequency in the population when  $g_c > g_d$ , which occurs when

$$\frac{B}{n} > C. \tag{10}$$

This is a standard result for the evolution of weak altruism in linear public goods games, i.e. social traits that increase the *absolute* fitness of the actor but increase the absolute fitness of other group members by even more (Wilson, 1975, 1979, 1990; Nunnery, 1985; Szathmary, 2011). Because all group members receive the benefit of cooperation, including the actor, then cooperation is selected for whenever the actor's share of the benefit exceeds the cost to itself. This depends on group size and is given by  $B/n > C$  (Figure 1a). This type of cooperation corresponds to what Pepper (2000) terms a whole-group trait. Biological examples of such whole-group traits include siderophore production in bacteria (Griffin et al., 2004), and the efficient use of shared resources through lower consumption rates (Pfeiffer et al., 2001; Kreft, 2004; Killingback et al., 2006). Whole-group traits also parallel the setup of economic public goods games (Fehr et al., 2002; Herrmann et al., 2008). For such traits a smaller group size favours cooperation because a cooperator receives a larger share of the benefits of its actions. In this model whenever  $B/n > C$ , cooperation fixes in the global population irrespective of starting frequency,

assuming deterministic evolution. For  $B/n < C$  defection fixes. An equivalent way of thinking about this is that for whole-group traits (such as public goods), the relatedness of actor to recipients in this population structure is  $1/n$ , assuming an infinite global population size (Pepper, 2000). Relatedness here is taken to mean a genetic correlation between actor and recipients at the locus for cooperation (Foster et al., 2006; West et al., 2007). The condition  $B/n > C$  is then an instance of Hamilton's rule (Hamilton, 1964).

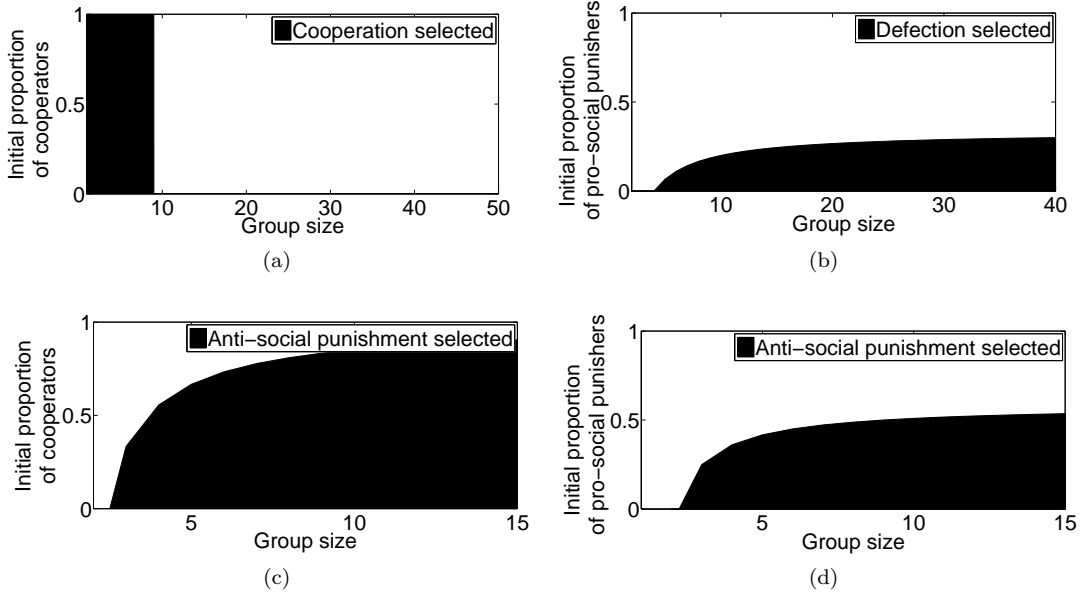


Figure 1: Analytical results of pairwise competition between strategies. Groups are formed by binomial sampling from the global population and disperse every generation (trait-group model). For this plot, parameters other than group size are fixed to the values used later in the simulations ( $B=0.9$ ,  $C=0.1$ ,  $K=0.1$ ,  $P=0.5$ ), c.f. main text. a) Non-punishing cooperators vs. non-punishing defectors. b) Pro-social punishers vs. non-punishing defectors. c) Anti-social punishers vs. non-punishing cooperators. d) Anti-social vs. pro-social punishers.

### 3.1.2. Pro-social punishers vs. non-punishing defectors

We next investigate the evolutionary dynamics of pro-social punishers compared to defectors. Recall that pro-social punishers are cooperators that identify individuals that defected, and then pay a fitness cost  $K$  to reduce the fitness of defectors in their group by  $P$ . From this we can derive the fitness of both strategies, given that they are placed in a group containing  $j$  pro-social punishers

$$\begin{aligned}
 w_p(j) &= B \frac{j+1}{n} - C - K \frac{n-(j+1)}{n} + 1 \\
 w_d(j) &= (B-P) \frac{j}{n} + 1
 \end{aligned} \tag{11}$$



As before, we assume that the distribution of strategies to groups is binomial;  $\mathbb{P}_n(j)$  is then the probability of being placed in a group with  $j$  pro-social punishers, given that groups are of size  $n$ . From this, we calculate the fitnesses of each individual:

$$\begin{aligned}
g_p &= \sum_{j=0}^{n-1} \mathbb{P}_n(j) w_p(j) \\
&= \sum_{j=0}^{n-1} \binom{n-1}{j} x_p^j (1-x_p)^{n-1-j} w_p(j) \\
&= x_p(B+K) \frac{n-1}{n} + \frac{B}{n} - C - K \frac{n-1}{n} + 1 \\
g_d &= \sum_{j=0}^{n-1} \mathbb{P}_n(j) w_d(j) \\
&= \sum_{j=0}^{n-1} \binom{n-1}{j} x_p^j (1-x_p)^{n-1-j} w_d(j) \\
&= x_p(B-P) \frac{n-1}{n} + 1,
\end{aligned} \tag{12}$$

where  $x_p$  is the global frequency of pro-social punishers. Pro-social punishment increases in proportion when  $g_p > g_d$ , or when

$$x_p > x_p^* = \frac{Cn - B}{(n-1)(P+K)} + \frac{K}{P+K}, \tag{13}$$

where  $x_p^*$  is the proportion of punishers needed in the population for punishment to be selectively favoured.  $x_p^*$  is horizontally asymptotic, with respect to group size  $n$ , with the asymptote at  $x_p^* = \frac{C+K}{P+K}$ . Figure 1b plots this critical value as function of  $n$ , the group size, using the parameters ( $B = 0.9$ ,  $C = 0.1$ ,  $K = 0.1$ ,  $P = 0.5$ ) that we later use in the simulations; we discuss robustness of the numerical results with respect to these parameters in Section 3.3. This result agrees with Equation 11 of Lehmann et al. (2007) (noting that we include the effect of a punisher on itself) for the case of randomly formed groups that disperse every generation, and applies where pro-social punishment and cooperation are perfectly linked traits. We relax these assumptions in the simulation model (Section 3.2).

### 3.1.3. Non-punishing cooperators vs. anti-social punishers

We now turn to investigate the dynamics of anti-social punishers in competition with non-punishing cooperators. In particular, we focus on whether anti-social punishment can prevent the invasion of cooperation even when  $B/n > C$ , i.e. even when the actor gains in absolute fitness terms from cooperating. The fitnesses in a group containing  $j$  cooperators are:

$$\begin{aligned}
w_c(j) &= B \frac{j+1}{n} - C - P \frac{n-(j+1)}{n} + 1 \\
w_a(j) &= (B-K) \frac{j}{n} + 1
\end{aligned} \tag{14}$$

Let  $g_c$  and  $g_a$  be the fitness of non-punishing cooperators and anti-social punishers respectively. Again let  $\mathbb{P}_n(j)$ , the probability of an individual being placed in a group with  $j$  cooperators, have a probability mass function of a binomially distributed random variable. Then

$$\begin{aligned}
g_c &= \sum_{j=0}^{n-1} \mathbb{P}_n(j) w_c(j) \\
&= \sum_{j=0}^{n-1} \binom{n-1}{j} x_c^j (1-x_c)^{n-1-j} w_c(j) \\
&= x_c(B+P) \frac{n-1}{n} + \frac{B}{n} - C - P \frac{n-1}{n} + 1 \\
g_a &= \sum_{j=0}^{n-1} \mathbb{P}_n(j) w_a(j) \\
&= \sum_{j=0}^{n-1} \binom{n-1}{j} x_c^j (1-x_c)^{n-1-j} w_a(j) \\
&= x_c(B-K) \frac{n-1}{n} + 1,
\end{aligned} \tag{15}$$

where  $x_c$  is the global proportion of cooperators. Cooperation thus increases in proportion when:

$$x_c > x_c^* = \frac{Cn - B}{(n-1)(P+K)} + \frac{P}{P+K}. \tag{16}$$

Critically, we see that cooperation can also *decrease* in proportion, even when  $B/n - C > 0$ . Figure 1c plots the critical value  $x_c^*$  against group size  $n$ . This has a horizontal asymptote at  $x_c^* = \frac{C+P}{P+K}$ .

### 3.1.4. Anti-social vs. pro-social punishers

Finally, we consider the dynamics of a population containing both pro- and anti-social punishers. As before, we let  $w_p(j)$ , and  $w_a(j)$  be the fitness of a pro-social punisher and an anti-social punisher in a group of size  $n$ , containing  $j$  pro-social punishers (excluding self). Then

$$\begin{aligned}
w_p(j) &= B \frac{j+1}{n} - C - (P+K) \frac{n-(j+1)}{n} + 1 \\
w_a(j) &= (B-K-P) \frac{j}{n} + 1
\end{aligned} \tag{17}$$

Let  $g_p$  and  $g_a$  be the fitness of each type after they have been placed into groups. The groups are again formed binomially. Then,

$$\begin{aligned}
g_p &= \sum_{j=0}^{n-1} \mathbb{P}_n(j) w_p(j) \\
&= \sum_{j=0}^{n-1} \binom{n-1}{j} x_p^j (1-x_p)^{n-1-j} w_p(j) \\
&= x_p(B+P+K) \frac{n-1}{n} + \frac{B}{n} - C - (P+K) \frac{n-1}{n} + 1 \\
g_a &= \sum_{j=0}^{n-1} \mathbb{P}_n(j) w_a(j) \\
&= \sum_{j=0}^{n-1} \binom{n-1}{j} x_p^j (1-x_p)^{n-1-j} w_a(j) \\
&= x_p(B-K-P) \frac{n-1}{n} +,
\end{aligned} \tag{18}$$

where  $x_p$  is the global proportion of pro-social punishers. Thus, punishment increases in proportion in the global population when

$$x_p > x_p^* = \frac{Cn - B}{2(n-1)(P+K)} + \frac{1}{2}. \tag{19}$$

This has a horizontal asymptote at  $x_p^* = \frac{C+K+P}{2(P+K)}$ . The critical initial frequency for pro-social punishment to be selected is plotted with respect to group size in Figure 1d.

### 3.1.5. Pro-social punishment vs. cooperation, anti-social punishment vs. defection, and the second-order free-riding problem

In the absence of other strategies, pro-social punishment is neutral with non-punishing cooperate. This is because in such a case there are no individuals to be punished, and hence the total cost of punishing is zero. Likewise, anti-social punishment is neutral with non-punishing defection in the absence of other strategies. However, all four strategies may always be present in above-zero frequency in a population due to mutation. In such cases the effects of pro-social punishment, in terms of reducing the proportion of defectors and anti-social punishers in the group, are shared equally by both pro-social punishers and non-punishing cooperators. Non-punishing cooperators, however, would not pay the cost of punishing and so would be expected to be fitter (the second-order public goods problem, Colman, 2006; Eldakar and Wilson, 2008). Similarly the effects of anti-social punishment, in terms of reducing the frequency of competing individuals with the cooperative trait, are felt equally by both anti-social punishers and non-punishing defectors in the same group. Non-punishing defectors, however, do not pay the cost of punishment. Thus, since in this model neither type of punishment differentially benefits punishers within a group, we might expect both types of punisher to be replaced by their non-punishing counterparts. Hence, we would not expect either type of punishment to be evolutionarily stable when non-punishing mutants are introduced. We investigate this through simulation in the next section.

### 3.2. Simulation results

For the primary simulation results below, we fix the migrant pool size at  $N = 500$ , the benefit of cooperation at  $B = 0.9$ , the cost of cooperation at  $C = 0.1$ , the cost of being punished at  $P = 0.5$ , the cost to the punisher at  $K = 0.1$ , and the mutation rate at  $\mu = 0.01$ . We vary the group size,  $n$ , and the number of generations before dispersal,  $T$ . We thus focus on the demographic factors that affect selection on punishment. We return to examining parameter sensitivity after presenting the primary results (Section 3.3).

As the analytic results above show, outcomes are sensitive to initial conditions, since selection pressures depend upon the frequencies of all four strategies (Equations 3–6). As a consequence, although a type may not be likely to invade when rare, it may be maintained or increase in frequency by selection when established at sufficient frequency. In this study, we focus on the initial condition where all four strategies are present in equal frequency. We address the validity of this assumption in the Discussion (Section 4). As we show below, from this state pro-social punishment and cooperation will be selected *against* in a well-mixed population. We therefore investigate how the presence of various types of group structure changes selection pressures on the maintenance of both types of punishment.

#### 3.2.1. Well-mixed population

We first investigate the effects of mutation in a well-mixed population. In the present model, we do this by setting  $n = N = 500$  and  $T = 1$ . With all four strategies started in equal frequency, both cooperate and pro-social punishment are driven extinct, apart from reintroduction by recurring mutation (fig. 2a). If anti-social punishment was neutral with non-punishing defect, we would expect both types to reach a proportion of approximately 50% under mutation. However, we see that anti-social punishment is in fact weakly selected against, being held at a frequency of around 40%. This is because anti-social punishers are paying the cost of punishing the few cooperators and pro-social punishers that are being reintroduced by mutation. The total cost of these acts of punishment is not large, however, because there are few individuals to punish and cooperators are selected against in a well-mixed population even without anti-social punishment (see analytical results, Section 3.1.1).

We next consider the case where pro-social punishment is initially fixed in the population. If only defectors (and anti-social punishers) arose by mutation, then pro-social punishment would be stable. However, we also allow for the possibility of non-punishing cooperators. In this situation, non-punishing cooperator mutants increase in frequency towards 50% (fig. 2b), as would be expected if pro-social punishment was neutral with non-punishing cooperation. However, the resulting decline in the frequency of pro-social punishment under mutation creates a second-order Tragedy of the Commons. That is, as pro-social punishment drops in frequency acts of punishment become too rare to prevent defection from being favoured; the condition for punishment to prevent defection in a well-mixed population ( $Px_p > Kx_d + C$ ) is then no longer met. The increase in non-punishing cooperators thus creates a selective environment that favours defection. This illustrates that pro-social punishment need not be stable in a well-mixed population when non-punishing mutants are introduced. We also note that this result holds even in the absence of anti-social punishment. Anti-social punishment thus plays no selective role in a well-mixed population, and is maintained at a frequency below that expected under neutrality with non-punishing defect.

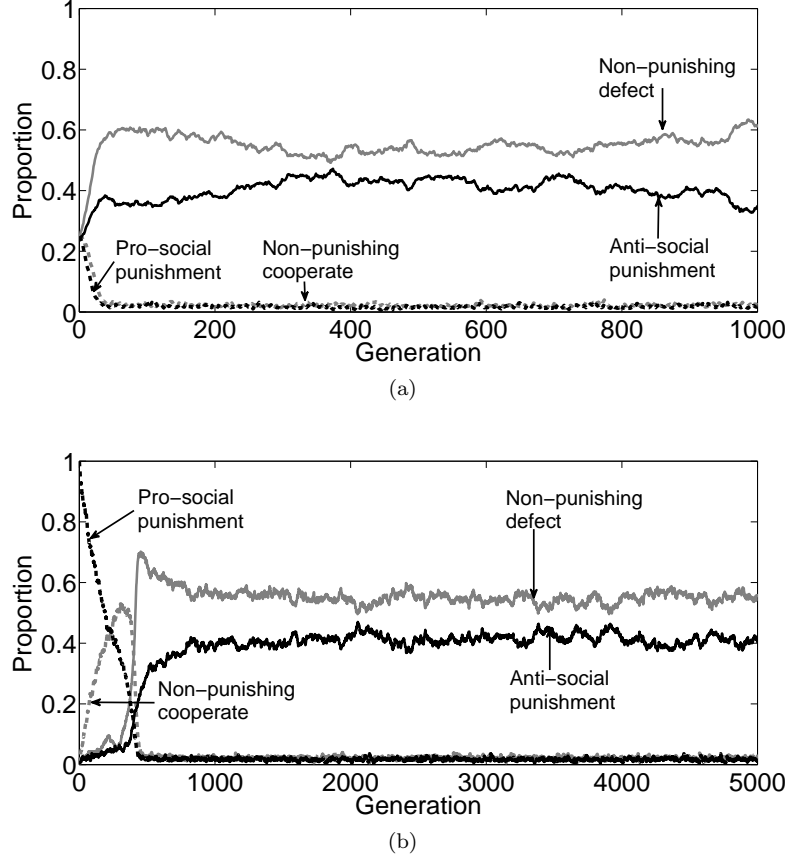


Figure 2: Simulation results of competition between pro-social punishers, anti-social punishers, non-punishing cooperators, and non-punishing defectors in a *well-mixed population* with mutation. a) All types initially present in equal frequency, showing the selective advantage of defection from this initial frequency. b) Pro-social punishment initially at fixation. Although stable as a strategy against invasion by defectors only (not shown), the increase in non-punishing cooperator mutants creates a second-order Tragedy of the Commons in which first pro-social punishment, and subsequently cooperation, collapses.

### 3.2.2. Effect of group size

We now consider the effects of group structure on the selective dynamics. We first vary group size, holding  $T = 1$ . With all four strategies started in equal frequency, we find that cooperation and pro-social punishment fix in the population for group sizes  $n < B/C$ . With  $B = 0.1$  and  $C = 0.9$ , in our model this is a group size less than 9. This is the classic result for randomly formed, single generational groups, *without punishment* (see analytical results). Thus, in this case allowing both cooperators and defectors to punish gives the same outcome as if neither type could punish. However, if the option of pro-social punishment is removed (by replacing all pro-social punishers

with non-punishing cooperators in the initial condition), but anti-social punishment is maintained, we find that the condition for cooperation to evolve is more stringent than  $n < B/C$ . Specifically, we found that cooperation only evolved for a group size less than 7. On the other hand, if anti-social punishment is removed from the initial condition (by replacing all anti-social punishers with non-punishing defectors), then cooperation and pro-social punishment can evolve even for group sizes where  $n > B/C$ . In terms of the parameters used in this study, pro-social punishment and cooperation reliably evolved in group sizes below 14, i.e. above the threshold of  $B/C = n = 9$ .

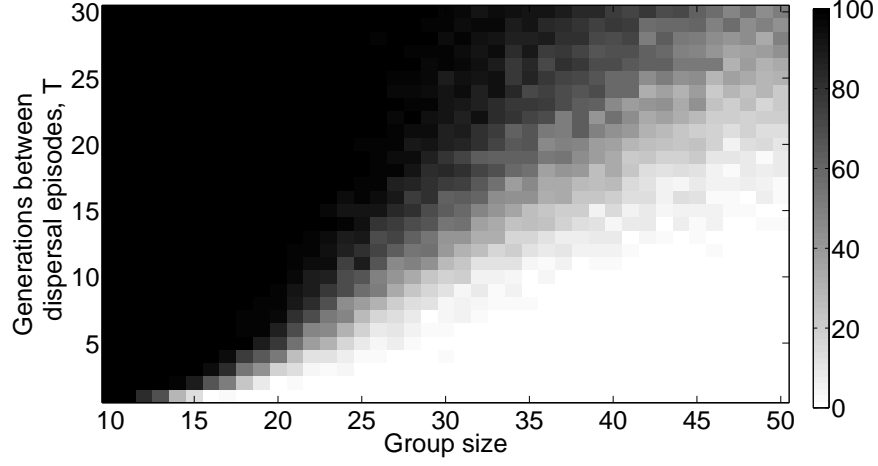
Importantly, when  $n > B/C$  then a whole-group trait that provides a fixed amount of benefit switches from being weakly to strongly altruistic (Pepper, 2000), or becomes “altruistic” in the sense used by Hamilton (1964) and more recently advocated by Lehmann and Keller (2006) and West et al. (2007). Such cooperation, when considered outside the context of punishment, causes an absolute reduction in the lifetime fitness of the actor. This illustrates that pro-social punishment can allow a cooperative trait that would otherwise be strongly altruistic to evolve in randomly formed groups. This occurs because pro-social punishment modifies the direct costs and benefits of cooperation, so that it is effectively no longer altruistic (Boyd and Richerson, 1992; Lehmann et al., 2007).

We also find that pro-social punishment and non-punishing cooperation form a stable polymorphic equilibrium in such cases, even in the presence of recurrent mutations. That is, the second-order Tragedy of the Commons does not occur in such group-structured populations. The reason for this, and the maintenance of pro-social punishment and cooperation even when  $n > B/C$ , is due to the fact that the population structure provides localised interactions. Specifically, mean fitness is lower in groups containing a greater proportion of defectors (Equations 3–6). Thus after dispersal such groups will make up a smaller fraction of the migrant pool, since the groups will contain fewer individuals relative to other groups after one iteration of Equation 7. For this to occur, different groups must contain different proportions of defectors when they are formed. That is, there must be variance in the composition of groups (Wilson, 1975). Since the groups are formed by random sampling, a smaller group size provides greater variance. Thus, smaller group sizes provide stronger selection against defection and anti-social punishment.

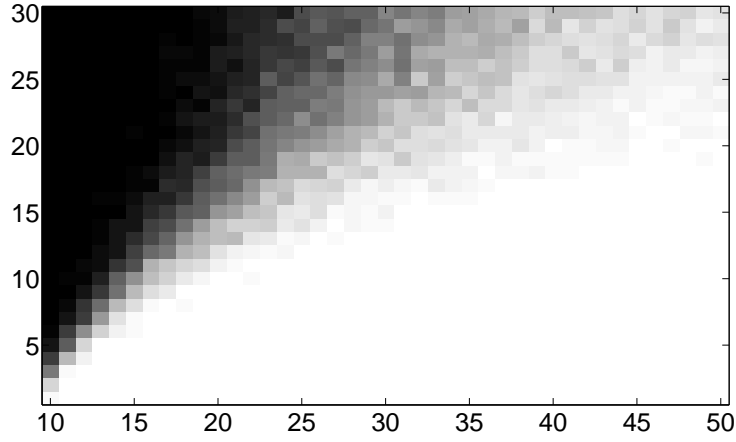
The results of this section illustrate that either type of punishment can prevent the evolution of a behaviour which would otherwise be selected given the population structure. They also illustrate that when both types of punishment are started in equal frequency their effects can be canceled out, with the population structure again becoming the determinant of selection on cooperation.

### 3.2.3. *Effect of dispersal frequency*

We next investigate varying the number of generations between dispersal episodes,  $T$ . We first consider the case in which anti-social punishment is removed, giving initial starting frequencies of 25% pro-social punishers, 25% non-punishing cooperators, and 50% non-punishing defectors. Figure 3a shows the effect of  $T$  on the largest group size for which the equilibrium is polymorphic for pro-social punishment and non-punishing cooperation, i.e. where defection is removed by selection. We took a simulation run to reach this equilibrium when the global proportion of pro-social punishers and cooperators exceeded 75% after 1000 cycles. The shading in the figure indicates the number of simulation runs, out of 100, which reached this equilibrium.



(a)



(b)

Figure 3: Effect of varying both group size and dispersal frequency. The shading indicates the number of simulation runs, out of 100, in which selection favoured pro-social punishment and cooperation after 1000 cycles. a) Without anti-social punishment; b) with anti-social punishment. Smaller group size increases variation in group composition, thus providing stronger selection against defection. Less frequent dispersal favours pro-social punishment by creating an equilibrium selection process. However, the addition of anti-social punishment reduces the largest group size under which pro-social punishment and cooperation are selected. Initial conditions for this simulation are given in the text.

The results show that the largest group size for which pro-social punishment and cooperation are selected increases with  $T$ . At first sight this result is surprising, since in

classic Haystack models without punishment a large  $T$  eliminates cooperation (Wilson, 1987; Sober and Wilson, 1998). This is because in such models there is only a single equilibrium within-groups: all defect. Thus, in the limit of  $T$  approaching infinity any group founded by at least one defector will be converted to all defect. Frequent dispersal can, though, keep the population out of this equilibrium and allow cooperation to be stable globally (Sober and Wilson, 1998). However, the addition of pro-social punishment to such models means that groups founded by one or more defectors need not, for high  $T$ , be converted to all defect.

For illustration, consider groups consisting of pro-social punishers and non-punishing defectors. Pro-social punishment is then a stable equilibrium within the group whenever the proportion of punishers causes the condition  $Px_p > Kx_d + C$  to be satisfied. Since a single group constitutes a well-mixed population, i.e. each group member interacts with all other group members with respect to public goods, this occurs above the limit of  $\frac{C+K}{P+K}$  (see analytical results). Under the parameters used in the simulations, this is when the fraction of pro-social punishers when the group is founded is greater than  $1/3$ . Groups founded by more than this proportion of pro-social punishers will thus be stable against defection. Thus, a high  $T$  need not cause an increase in defection within each group. Moreover, individuals in groups at the pro-social punishment equilibrium have a higher mean fitness, due to the benefits of cooperation (Equations 4–5). The more generations the group stays together for, the greater the cumulative total of this benefit compared to non-cooperation groups, since groups grow at an exponential rate (with no negative density-dependent effects) in accordance with Equation 7. Consequently, when dispersal eventually occurs groups at the pro-social punishment equilibrium will have grown to a larger size, and will hence make up a larger fraction of the migrant pool.

A larger  $T$  can thus favour pro-social punishment, due to the reproductive advantage that individuals in groups at the pro-social punishment equilibrium enjoy with each generation that the group stays together. This mechanism depends upon some groups being founded with type frequencies that fall within the basin of attraction for the pro-social punishment equilibrium, i.e. with  $x_p > 1/3$ . This can occur in a group-structured population even when the global value of  $x_p$  is below this (i.e. 0.25 as used in the simulations), provided there is variance in the composition of groups when they are founded. In our model, this variance is provided through the formation of groups by hypergeometric (random) sampling of individuals from the migrant pool. This variance decreases, however, as the founding size of the groups becomes larger. Thus for larger group sizes, fewer groups lie in the basin of attraction for the pro-social punishment equilibrium. This explains why for large group sizes, a large  $T$  may not be sufficient to select for pro-social punishment, because too few (or no) groups may fall in its basin of attraction.

Finally, we consider the effects of varying  $T$  as well as group size when anti-social punishment is added to the model. In Figure 3b we use the same parameters as in Figure 3a, but here we reintroduce anti-social punishment, returning to the initial condition in which all four strategies are at 25%. In this case we see that pro-social punishment and cooperation are selected over a much smaller range of group sizes for a given dispersal frequency. As  $T$  is increased, the increase in the largest group size under which pro-social punishment and cooperation are selected is also less pronounced.

The reason for this result is that the basin boundary for the pro-social punishment equilibrium changes within a group. In particular, from the analytical results we know that in a single group founded by pro-social punishers and anti-social punishers only, the



basin boundary lies at  $x_p = 1 - \frac{C+K+P}{2(P+K)}$ , which is a more stringent condition than the population without anti-social punishment ( $\frac{C+K}{P+K}$ ). Under the parameters used in the simulation, this corresponds to  $x_p > 1/3$  without anti-social punishment, and  $x_p > 5/12$  in the presence of anti-social punishment. We verified numerically that this result holds in the four-type system when the three other types are all started in equal proportion. Thus for a given frequency of pro-social punishment in the migrant pool, fewer groups are expected to fall in the basin of attraction for the pro-social punishment equilibrium when some of the non-punishing defectors are replaced with anti-social punishers. The presence of anti-social punishment therefore means that a larger between-group variance (relative to the migrant pool value of  $x_p$ ) is required to select for pro-social punishment.

### 3.3. Sensitivity to the effect-to-cost ratio of cooperation and punishment

The benefit-to-cost ratio of the cooperative act affects the largest group size in which cooperation can evolve. Without either type of punishment, when  $T = 1$  then cooperation is selectively advantageous when  $B/n > C$ ; this is the well-known result from Wilson's (1975) trait-group model when groups are formed randomly. When both pro- and anti-social punishment are available, and all four strategies are initially present in the population at equal frequency, then our simulations shows that the effects of both type of punishment on the level of cooperation cancel out. In other words, the condition for cooperation to be favoured is still  $B/n > C$  when both types of punishment are added and  $T = 1$ . We find this result to be insensitive to the effect-to-cost ratio of punishment; it holds in the simulations even for  $P = K = 0.1$ , as well as for  $P > K$ .

For  $T > 1$ , we find that the addition of anti-social punishment reduces the largest group size over which cooperation evolves, compared to the case where only pro-social punishment was available. This result is also qualitatively insensitive to the benefit-to-cost ratio of cooperation. That is, decreasing the benefit-to-cost ratio of cooperation decreases the largest group size in which cooperation evolves in the case where both anti- and pro-social punishment are present, and similarly in the case where only pro-social punishment is available. The result that anti-social punishment further reduces this over the pro-social punishment only case, however, still holds regardless of the  $B/C$  ratio when  $K = 0.1$  and  $P = 0.5$ . Further, we found that increasing  $P$  (while holding  $K$  constant) increases the magnitude of this effect. That is, the addition of anti-social punishment makes a greater difference as  $P$  increases. As  $P$  decreases, however, both types of punishment have less effect and the difference between the two cases becomes smaller. When  $K = 0.1$  and  $P < 0.4$ , we found that the addition of anti-social punishment made no difference to the range of group sizes over which cooperation evolves, compared to the case where only pro-social punishment is available.

It should be noted that  $P > K$  is a common assumption in both models of the evolution of punishment (e.g. Boyd et al. 2003, 2010; Bowles and Gintis 2004; Lehmann et al. 2007; dos Santos et al. 2011), and in experimental public goods games (Fehr et al., 2002; Herrmann et al., 2008). Nevertheless, measuring the actual cost-to-effect ratio of punishment *in situ* in real populations is very difficult. Indeed, some authors have explicitly considered the case where  $P = K$  (Rand et al., 2010). However, at least in the case of humans it is commonly held that the advent of tools from gossip to weaponry makes punishment very effective at little cost to the punisher (Sober and Wilson, 1998; Bingham, 1999; Boehm, 1999; Binmore, 2005). We have thus focused our study on cases where

punishment is reasonably efficient in terms of effect-to-cost ratio, whilst still being less efficient than the benefit-to-cost ratio of the cooperative act.

#### 4. Discussion and conclusion

We have presented here, to our knowledge, the first model of the evolution of anti-social punishment in group-structured populations. Previous work on anti-social punishment has nevertheless suggested that group structure would favour pro-social punishment and prevent anti-social punishment from being effective (Rand et al., 2010; Rand and Nowak, 2011). Further, much previous work on the evolution of pro-social punishment in group-structured populations has not even considered the possibility of anti-social punishment (e.g. Boyd et al. 2003, 2010; Gardner and West 2004; Lehmann et al. 2007), presumably for the same reason. After all, group or kin selection should be expected to promote behaviours that support cooperation rather than defection, assuming a population structure that provides positive relatedness at the locus for cooperation (Hamilton, 1964; Wilson, 1975).

In fact, we have shown here that anti-social punishment *can* be effective in the preventing the evolution of pro-social punishment and cooperation in group-structured populations. Models for the evolution of pro-social punishment typically rely both on pro-social punishment being a stable equilibrium within a group, and on some groups being founded with initial strategy frequencies that fall within the basin of attraction for this equilibrium. When these two conditions are met, equilibrium selection between groups can occur (Harsanyi and Selten, 1988; Boyd and Richerson, 1990; Binmore, 1998; Canals and Vega-Redondo, 1998), such that groups at the pro-social punishment and cooperation equilibrium out-compete those at the defection equilibrium (Boyd et al., 2003). We have shown here that the presence of anti-social punishers reduces the likelihood of the second condition being met, by reducing the basin of attraction for the pro-social punishment equilibrium, compared to a population where the anti-social punishers are replaced with non-punishing defectors. Consequently, a greater between-group variance in the frequency of pro-social punishment is required in order for some groups to fall in its basin of attraction, and equilibrium selection to occur.

One way such a greater between-group variance can be achieved is through a reduction in group size. However, such a requirement eliminates punishment as an explanation for the maintenance of cooperation in large human groups with low relatedness. Notice though that the results in this model assume that there is no structure to a society *within* a large group. However, internal structure within large groups may in fact be present e.g. due to social hierarchy or spatial distribution of public goods. Nevertheless, the homogeneity of within-group structure is a standard assumption in group-structured models of the evolution of cooperation (Boyd and Richerson, 1990; Boyd et al., 2003, 2010; Wilson, 1975, 1987; Hamilton, 1975; Traulsen and Nowak, 2006; Lehmann et al., 2007), and corresponds to a public good that is shared equally with all group members. Moreover, if the effective group size of social interactions is smaller then pro-social punishment may not be necessary to maintain cooperation anyway; direct and indirect fitness benefits from the cooperative act itself may be sufficient. We have thus focused here on cases where the public good is shared equally between all group members and hence pro-social punishment *is* necessary to maintain cooperation in large groups. For the same reason, we have also focused on linear public goods games. This is because in

non-linear public goods games, punishment would not be needed to maintain cooperation even in large randomly formed groups (Archetti and Scheuring, 2012). Whether real-life social dilemmas are linear or non-linear is an empirical question that must be answered on a case by case basis.

It is worth stressing that we have considered the *maintenance* of punishment, rather than its invasion from mutation frequency. It is already widely appreciated that punishment can be stable when common, even if it is not selected when rare (Boyd and Richerson, 1992; Lehmann et al., 2007). This is because in the standard model, the total individual cost of punishment decreases as punishers increase in frequency within a group (Equations 3–6). Thus, both pro- and anti-social punishment undergo positive frequency-dependent selection. In light of this, much work has focused on the maintenance of punishment (e.g. Boyd and Richerson 1992; Henrich and Boyd 2001; Gintis et al. 2003), as we do in this study. Several mechanisms have, however, been suggested for the invasion of (pro-social) punishment from rarity. These include kin benefits resulting from punishing acts reducing local competition (Lehmann et al., 2007), the fixation of punishment within a single group through stochastic processes (Boyd et al., 2003), voluntary participation in social interactions (Hauert et al., 2007), systems of reputation (dos Santos et al., 2011), or the coordination of punishing behaviour between individuals (Boyd et al., 2010). It has been shown more generally that social traits which are maladaptive when rare, but advantageous once common, may be able to reach the threshold frequency for positive selection by drift-like processes (Boyd and Richerson, 1990; Boyd et al., 2003). One mechanism by which this may occur is when environmental factors result in population oscillations, and periods where the environment is temporarily below its maximum carrying capacity (Čače and Bryson, 2007; Alizon and Taylor, 2008).

Similarly, future studies should investigate the proximate mechanisms by which anti-social punishment might be favoured over simple non-punishing defection within a single group. This is similar to the classic problem of how pro-social punishers may be favoured over non-punishing cooperators within a single group (Colman, 2006). Essentially, either type of punishment can be favoured if the effects of punishment are not shared equally with non-punishers in the same group, but instead feed disproportionately back to the actor or their kin. As mentioned earlier, it is difficult to imagine direct advantage from anti-social punishment, at least as described here and in the economics literature. However, a linked consequence such as increased social status may serve as the explanatory benefit.

In conclusion, we have shown here that the presence of anti-social punishers reduces the range of conditions over which pro-social punishment and cooperation are stable in group-structured populations. This occurs because anti-social punishment reduces the basin of attraction for the pro-social punishment equilibrium within groups. Thus, a given magnitude of between-group variance may no longer be sufficient to select for pro-social punishment. In particular, we have shown here how the range of group sizes over which pro-social punishment is selected can be greatly reduced by anti-social punishment. Given the existence of anti-social punishment in all studied extant human cultures (Herrmann et al., 2008; Sylwester et al., 2011), our results suggest that the claims of models showing the evolution of pro-social punishment in group-structured populations should be re-evaluated with the addition of anti-social punishment.

## Acknowledgments

We thank Laurent Lehmann, and members of the AmonI group at the University of Bath — particularly Karolina Sylwester — for useful discussions. We also thank Marco Archetti and an anonymous reviewer for helpful feedback, and Slimane Dridi and Jorge Peña for comments on a draft of the manuscript. This effort was sponsored by the US Air Force Office of Scientific Research, Air Force Material Command, USAF, under grant number FA8655-10-1-3050.

## References

- Alizon, S., Taylor, P., 2008. Empty sites can promote altruistic behaviour. *Evolution* 62 (6), 1335–1344.
- Anderson, C. M., Putterman, L., 2006. Do non-strategic sanctions obey the law of demand? The demand for punishment in the voluntary contribution mechanism. *Game. Econ. Behav.* 54 (1), 1–24.
- Archetti, M., Scheuring, I., 2012. Review: Game theory of public goods in one-shot social dilemmas without assortment. *J. Theor. Biol.* 299, 9–20.
- Bergstrom, T. C., 2002. Evolution of social behavior: Individual and group selection. *J. Econ. Perspect.* 16 (2), 67–88.
- Bingham, P., 1999. Human uniqueness: a general theory. *Q. Rev. Biol.*, 133–169.
- Binmore, K., 1998. *Just Playing: Game Theory and the Social Contract*. Vol. 2. MIT press.
- Binmore, K., 2005. *Natural Justice*. Oxford University Press.
- Boehm, C., 1999. *Hierarchy in the Forest: The Evolution of Egalitarian Behavior*. Harvard Univ Pr.
- Bowles, S., Gintis, H., 2004. The evolution of strong reciprocity: cooperation in heterogeneous populations. *Theor. Popul. Biol.* 65 (1), 17–28.
- Boyd, R., Gintis, H., Bowles, S., 2010. Coordinated punishment of defectors sustains cooperation and can proliferate when rare. *Science* 328 (5978), 617.
- Boyd, R., Gintis, H., Bowles, S., Richerson, P. J., 2003. The evolution of altruistic punishment. *Proc. Natl. Acad. Sci. U. S. A.* 100 (6), 3531–3535.
- Boyd, R., Richerson, P., 1992. Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethol. Sociobiol.* 13 (3), 171–195.
- Boyd, R., Richerson, P. J., 1990. Group selection among alternative evolutionarily stable strategies. *J. Theor. Biol.* 145, 331–342.
- Canals, J., Vega-Redondo, F., 1998. Multi-level evolution in population games. *International Journal of Game Theory* 27 (1), 21–35.
- Cohen, D., Eshel, I., et al., 1976. On the founder effect and the evolution of altruistic traits. *Theor. Popul. Biol.* 10 (3), 276.
- Colman, A., 2006. The puzzle of cooperation. *Nature* 440 (7085), 744–745.
- dos Santos, M., Rankin, D., Wedekind, C., 2011. The evolution of punishment through reputation. *Proc. R. Soc. Biol. Sci. Ser. B* 278 (1704), 371–377.
- Eldakar, O. T., Wilson, D. S., 2008. Selfishness as second-order altruism. *Proceedings of the National Academy of Sciences* 105 (19), 6982–6986.
- Fehr, E., Fischbacher, U., Gächter, S., 2002. Strong reciprocity, human cooperation, and the enforcement of social norms. *Hum. Nature-int. Bios.* 13 (1), 1–25.
- Fletcher, J. A., Zwick, M., 2004. Strong altruism can evolve in randomly formed groups. *J. Theor. Biol.* 228, 303–313.
- Fletcher, J. A., Zwick, M., 2007. The evolution of altruism: Game theory in multilevel selection and inclusive fitness. *J. Theor. Biol.* 245 (1), 26–36.
- Foster, K. R., Wenseleers, T., Ratnieks, F. L., 2006. Kin selection is the key to altruism. *Trends Ecol. Evol.* 21 (2), 57–60.
- Frank, S. A., 1998. *Foundations of Social Evolution*. Monographs in Behavior and Ecology. Princeton University Press, Princeton.
- Gardner, A., West, S., 2004. Cooperation and punishment, especially in humans. *Am. Nat.* 164 (6), 753–764.
- Gintis, H., Bowles, S., Boyd, R., Fehr, E., 2003. Explaining altruistic behavior in humans. *Evol. Hum. Behav.* 24 (3), 153–172.
- Griffin, A. S., West, S. A., Buckling, A., 2004. Cooperation and competition in pathogenic bacteria. *Nature* 430, 1024–1027.

- Hamilton, W. D., 1964. The genetical evolution of social behaviour. I. *J. Theor. Biol.* 7 (1), 1–16.
- Hamilton, W. D., 1975. Innate social aptitudes in man, an approach from evolutionary genetics. In: Fox, R. (Ed.), *Biosocial Anthropology*. Malaby Press, pp. 133–155.
- Hammerstein, P., 2003. *Genetic and Cultural Evolution of Cooperation*. MIT Press.
- Hardin, G., 1968. The tragedy of the commons. *Science* 162, 1243–1248.
- Harsanyi, J. C., Selten, R., 1988. *A General Theory of Equilibrium Selection in Games*. MIT Press, Cambridge, MA.
- Hauert, C., Traulsen, A., Brandt, H., Nowak, M., Sigmund, K., 2007. Via freedom to coercion: the emergence of costly punishment. *Science* 316 (5833), 1905–1907.
- Henrich, J., Boyd, R., 2001. Why people punish defectors: Weak conformist transmission can stabilize costly enforcement of norms in cooperative dilemmas. *J. Theor. Biol.* 208 (1), 79–89.
- Herrmann, B., Thöni, C., Gächter, S., 2008. Antisocial punishment across societies. *Science* 319 (5868), 1362.
- Killingback, T., Bieri, J., Flatt, T., 2006. Evolution in group-structured populations can resolve the tragedy of the commons. *Proc. R. Soc. Biol. Sci. Ser. B* 273, 1477–1481.
- Kreft, J.-U., 2004. Biofilms promote altruism. *Microbiology* 150, 2751–2760.
- Lehmann, L., Keller, L., 2006. The evolution of cooperation and altruism - a general framework and a classification of models. *J. Evol. Biol.* 19 (5), 1365–1376.
- Lehmann, L., Rousset, F., Roze, D., Keller, L., 2007. Strong reciprocity or strong ferocity? A population genetic view of the evolution of altruistic punishment. *Am. Nat.* 170 (1), 21–36.
- Mathew, S., Boyd, R., 2011. Punishment sustains large-scale cooperation in prestate warfare. *Proc. Natl. Acad. Sci. U. S. A.* 108 (28), 11375.
- Maynard Smith, J., 1964. Group selection and kin selection. *Nature* 201, 1145–1147.
- Maynard Smith, J., Szathmáry, E., 1995. *Major Transitions in Evolution*. W. H. Freeman/Spektrum, Oxford.
- Michod, R. E., 1983. Evolution of the first replicators. *American Zoology* 23, 5–14.
- Nunney, L., 1985. Group selection, altruism, and structured-deme models. *Am. Nat.* 126 (2), 212–230.
- Okasha, S., 2006. *Evolution and the Levels of Selection*. Clarendon Press.
- Pepper, J. W., 2000. Relatedness in trait group models of social evolution. *J. Theor. Biol.* 206 (3), 355–368.
- Pfeiffer, T., Schuster, S., Bonhoeffer, S., 2001. Cooperation and competition in the evolution of ATP-producing pathways. *Science* 292 (5516), 504–507.
- Powers, S. T., Penn, A. S., Watson, R. A., 2011. The concurrent evolution of cooperation and the population structures that support it. *Evolution* 65 (6), 1527–1543.
- Rand, D., Armao IV, J., Nakamaru, M., Ohtsuki, H., 2010. Anti-social punishment can prevent the co-evolution of punishment and cooperation. *J. Theor. Biol.* 265 (4), 624–632.
- Rand, D., Nowak, M., 2011. The evolution of antisocial punishment in optional public goods games. *Nature Communications* 2, 434.
- Santos, M., Szathmáry, E., 2008. Genetic hitchhiking can promote the initial spread of strong altruism. *BMC Evol. Biol.* 8 (281).
- Sober, E., Wilson, D. S., 1998. *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Harvard University Press, Cambridge, MA.
- Sylwester, K., Herrmann, B., Bryson, J. J., 2011. *Homo homini lupus?* an evolutionary view on antisocial punishment., under review.
- Szathmáry, E., 2011. To group or not to group? *Science* 324 (19), 1648–1649.
- Traulsen, A., Nowak, M., 2006. Evolution of cooperation by multilevel selection. *Proc. Natl. Acad. Sci. U. S. A.* 103 (29), 10952–10955.
- Čače, I., Bryson, J., 2007. Agent based modelling of communication costs: Why information can be free. In: Lyon, C., Nehaniv, C. L., Cangelosi, A. (Eds.), *Emergence and Evolution of Linguistic Communication*. Springer, London, pp. 305–322.
- West, S., Griffin, A., Gardner, A., 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J. Evol. Biol.* 20, 415–432.
- Wilson, D. S., 1975. A theory of group selection. *Proc. Natl. Acad. Sci. U. S. A.* 72 (1), 143–146.
- Wilson, D. S., 1979. Structured demes and trait-group variation. *Am. Nat.* 113 (4), 606–610.
- Wilson, D. S., 1987. Altruism in mendelian populations derived from sibling groups: The Haystack model revisited. *Evolution* 41 (5), 1059–1070.
- Wilson, D. S., 1990. Weak altruism, strong group selection. *Oikos* 59 (1), 135–140.